REPRODUCTION OF THE POLYCHAETE GLYCERA DIBRANCHIATA AT SOLOMONS, MARYLAND [1]

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Remarkably little is known about the life history and the ecology of the errant polychaete family Glyceridae. Basic information of this nature is needed not only to allow a synthesis of such isolated data as are presently available, but also to provide the background necessary for experimental investigations. In view of this, the work of Klawe and Dickie (1957) on *Glycera dibranchiata* Ehlers in the Maritime Provinces is of particular interest, since it appears to be the only publication dealing with the biology of a glycerid worm. Commonly known as the "bloodworm" or "beak-thrower," this species is a favorite bait of salt-water sport fishermen, whose demand has made it of some commercial importance in Maine and the Maritime Provinces. The studies of Klawe and Dickie were undertaken to obtain information relating to questions of bloodworm conservation, and their report contains many original observations. But the chief value of their contribution lies, perhaps, not so much in its extensive data as in its indication of the numerous problems still requiring considerable study.

Of particular importance are the gaps persisting in our knowledge of glycerid reproduction, many aspects of which have remained largely a matter of conjecture. It is with these deficiencies in the case of *Glycera dibranchiata* that the present study is concerned. Intended to enlarge upon the work of Klawe and Dickie, this report deals with the breeding season, swarming and epitoky of *G. dibranchiata* in more southern waters, and uses histological findings to supplement field observations. Gametogenesis and early development will be considered in a separate paper.

METHODS

Most of the information presented here is based on work conducted at the Chesapeake Biological Laboratory at Solomons, Maryland, from the last week of June, 1960, to the early part of February, 1961. Unless otherwise stated, all specimens were collected from the waters immediately surrounding Solomons Island, situated in the mouth of the Patuxent River, about two miles from its entrance into Chesapeake Bay (Fig. 1). Some of the hydrographic features of this area have been described by Nash (1947) and Beaven (1960). Since the
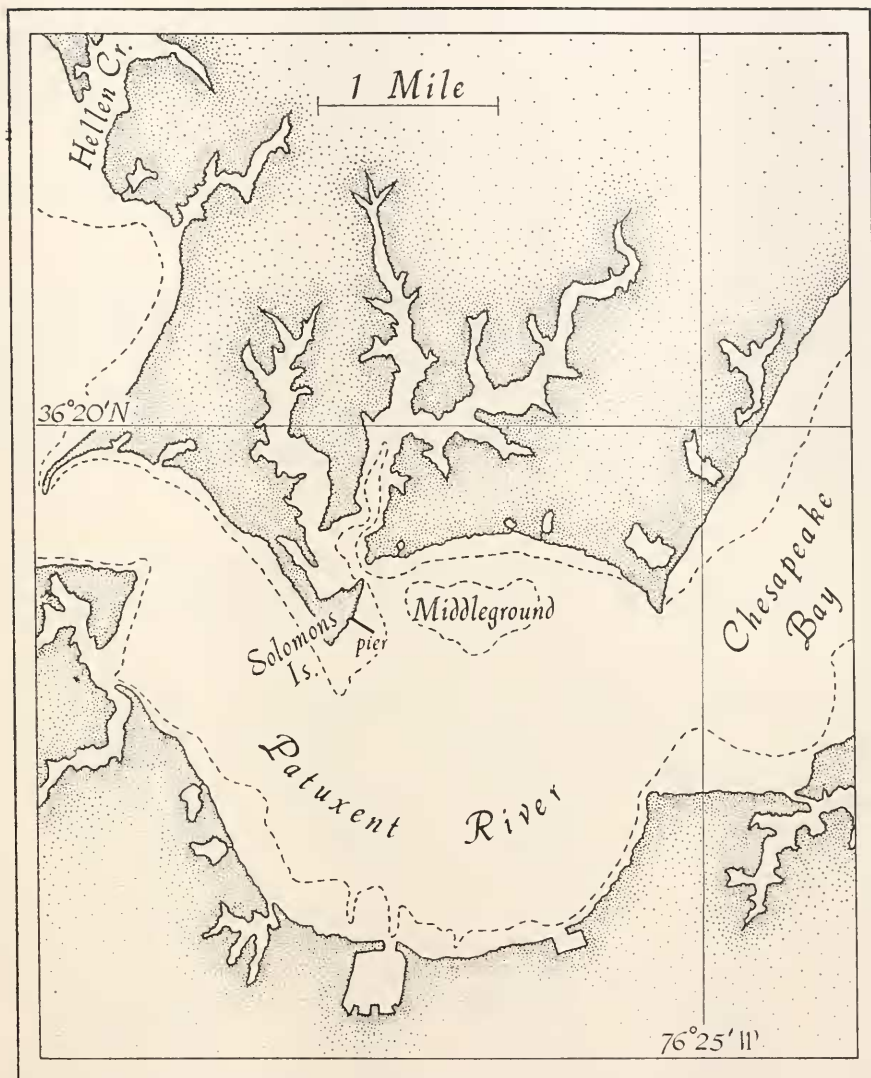
FIGURE 1. Location of Solomons Island and other areas mentioned in the text. Broken line indicates the 12-foot bottom contour.

mean tidal amplitude at Solomons is only 1.2 feet, there is practically no inter-tidal zone; all collecting, therefore, was done with a Maryland soft clam dredge (see Manning, 1959), operated in 6–10 feet of water. This method, using a wire mesh conveyor belt to bring specimens up from the bottom, proved satis-factory for obtaining 2–4 dozen uninjured worms in a relatively short period of time.

Living worms narcotized in magnesium chloride were measured by the method

of Klawe and Dickie, who used a watertight trough, V-shaped in cross-section, with a ruler attached to one side. Some measurements were obtained from fixed material and will be so indicated. Narcotized animals were fixed in Bouin's fluid and stored in a preservative consisting of 2 parts ethyl alcohol, 1 part distilled water and 1 part glycerine. For general examination, paraffin sections 4–7 μ thick were stained in Ehrlich's hematoxylin and eosin.

Other methods used in connection with specific problems will be described in the appropriate sections.

BREEDING SEASON

Table I summarizes the available information on reproductive periods in several species of *Glycera*. For *G. dibranchiata,* Klawe and Dickie have indicated mid-May as the probable time of maximum reproduction in Nova Scotia and Maine. The present study was begun near the end of June, too late to determine the presence or absence of a spring spawning. Other records, however, suggested the possibility of a second breeding season for this species at Solomons, and an autumn spawning did in fact occur.

Previous reports for Solomons

Three earlier reports of breeding activity for *Glycera* were found in records at the Chesapeake Biological Laboratory. One of these is a brief anonymous note

TABLE I

Breeding seasons of Glycera *species*

Species	Locality	Time of year	Evidence	Source
G. alba	The Sound	Late autumn?	Larvae in winter	Thorson, 1946
G. americana	Woods Hole Maryland Solomons	Summer Spring–Summer December	Adults at surface Swarming Swarming	Pettibone (in press) Anonymous, 1948 Beaven (see text)
G. capitata	Norway	May–July	Epitokes at surface	Støp-Bowitz, 1941
G. convoluta	Naples Algiers Plymouth	May April June–August	Spawning Epitoke at surface Ripe gametes	Lo Bianco, 1909 Gravier and Dantan, 1928 Fuchs, 1911
G. dibranchiata	Woods Hole Maine and Canada Maryland Solomons Solomons Solomons	August; January April–June Spring–Summer July November December	Adults at surface Ripe gametes Swarming Swarming Swarming Swarming epitokes	Pettibone (in press) Klawe and Dickie, 1957 Anonymous, 1948 Myers (see text) Beaven (see text) This paper
G. lapidum	Algiers Concarneau Norway and Sweden	February December–April August?	Epitoke at surface Epitokes at surface Pre-epitokes in July Young in September	Gravier and Dantan, 1928 Fage and Legendre, 1927 Støp-Bowitz, 1941 Arwidsson, 1898
G. nana	British Columbia	Autumn	Swarming	Berkeley and Berkeley, 1948
G. robusta	Monterey Bay	Spring–Summer	Ripe gametes	MacGinitie, 1935
G. rouxii	Concarnean Banyuls Norway and Sweden	October August October?	Epitoke at surface Epitoke at surface Pre-epitokes in September	Fage and Legendre, 1927 Fage and Legendre, 1927 Støp-Bowitz, 1941
G. siphonostoma	Naples	December–April	Mature adults	Lo Bianco, 1909
G. ?sphyrabrancha	Puerto Rico	October	Ripe adults at surface	Allen, 1957
G. tesselata	Algiers	October–November	Epitokes at surface	Gravier and Dantan, 1928

appearing in a 1948 issue of the Maryland Tidewater News and describing swarming of these worms "in the tidal waters of Maryland" during late spring and early summer of each year. It also states (p. 4) that "there are two species of *Glycera* found along our coast, both of which carry on the curious antics reported above." Presumably the species referred to would be *G. dibranchiata* and *G. americana*. The other two reports of swarming were found in a card file of invertebrates occurring near Solomons. One gives the following information: "*Glycera dibranchiata;* large numbers swimming off CBL pier, presumably this species; one specimen identified; July 15 [no year]; Marvin Myers." The other entry reports *G. dibranchiata* swarming in the same area on the nights of December 4–7, 1944; apparently *G. americana* was also present the first of these nights. In none of these cases has it been possible to verify the identity of the worms. The December, 1944, swarms, however, were witnessed by Mr. Francis Beaven, currently a member of the Laboratory staff, who was able to provide some further details concerning the event. There seems little reason to question that in this case, at least, the generic identification was correct. If the benefit of the doubt is extended to the other two reports, it must be concluded that *Glycera* has two breeding periods a year in this locality.

Rate of sexual development

Between late June, 1960, and swarming time in early November, 75% of the worms examined histologically had gonads in various stages of development. These specimens, 55 in all, represent ten samples taken the following numbers of days before the first swarm: 129, 90, 77, 70, 58, 45, 36, 16, 8 and 4. Relaxed length of the worms ranged from 7 to 26 cm., with the majority falling into the 16–20 cm. group. Although these limited samples allow only tentative generalization, two observations should be mentioned. First, there seemed to be no correlation between specimen length and presence of gonads, though the gonads of shorter worms were generally smaller. Secondly, contrary to expectation, the frequency of mature specimens in each sample diminished as swarming time drew closer. This could, perhaps, indicate a migration of mature worms away from the usual collecting area into shallower water, where swarming appeared to be more concentrated. But both of these observations need to be checked by statistical treatment of larger samples.

The earliest definite sign of approaching maturity occurred in mid-September, 45 days before swarming. Two of the specimens fixed then contained sperm plates and a third contained eggs in the coelom. The appearance and the small number of these free gametes suggested that their release from the gonads had just recently begun. This agrees reasonably well with the observations of Klawe and Dickie, who found immature eggs free in the coelom of some worms in late August. Evidence of a more advanced degree of maturity appeared about one month later, in a specimen fixed 16 days before swarming. This was a female with eggs almost completely filling the body cavity and with no remaining gonad tissue. The atrophy of the gut and body wall that accompanies sexual maturity had already begun but was not yet pronounced. The sample collected four days before swarming included worms in final stages of maturation. Two females and one male shed gametes when handled in the laboratory. Although the sperm plates released by the male did not break up

into individual sperm, some of the gametes must have been ripe, since an attempt at fertilization gave a small number of cleaving eggs that developed into swimming blastulae.

If biannual reproduction is assumed, these observations may be tentatively interpreted as follows: Of the worms collected in summer, those with well developed gonads probably represented the fall breeders of 1960; those with poorly developed gonads, the spring or summer breeders of 1961; and those with no gonads, the fall breeders of 1961. It would then follow that complete sexual development requires about one year. The observations also indicate that young gametes of both sexes are released from the gonads into the coelom at approximately the same time and ripen within the following 6 to 8 weeks.

Length of breeding season

It is difficult at present to suggest the limits of the reproductive seasons at Solomons. Both the anonymous article and Myers' notation indicate that the earlier period may center around June and July. The fact that no mature worms were found at the beginning of the present study (the end of June) is not incompatible with this suggestion. If actual spawning is of short duration, a matter of a few days to a week, then it could have taken place in its entirety during the early part of June. Furthermore, it has already been mentioned that mature worms became scarcer in samples dredged nearer the time of swarming; thus it is possible that the number of mature worms had similarly decreased in the collecting area during late June. Any swarming activity that might have occurred in June or July could easily have been overlooked. The information available for the autumn breeding season is more definite, though still insufficient to form any hard and fast conclusions. In both cases, namely December, 1944, and November, 1960, observed swarming was limited to four successive days. Whether this coincidence is purely fortuitous, or whether it reflects a high degree of reproductive synchrony cannot at present be settled. Nor is there any way to determine that these were the only spawning events during the fall months of 1944 and 1960.

Environmental factors

Temperature conditions of surface water at Solomons for a 20-year period have been summarized by Beaven (1960). These records show mean temperatures ranging from 3.3° C. in February to 26.7° C. in August, with extremes of −0.8 and 31° C. The greatest difference between surface and bottom temperature occurs in the spring, when readings may be about three degrees lower at 17 feet (Nash, 1947), and eight degrees lower at 60 feet (Beaven, 1960). During the fall months water is generally slightly warmer at the bottom than at the surface. There appears to be little correlation between absolute temperature and the suggested breeding periods, except that temperature is approaching its maximum during June and July, and its minimum during November and December. In the two-week period before swarming, water temperature fell gradually from 10.3 to 5.5° C. in 1944, and from 18.7 to 13.8° C. in 1960. The average daily difference was −0.36° C. in both years, but this is of questionable significance. Otherwise the data suggest only that final sexual maturity can be attained within a fairly wide temperature range.

Two attempts were made at Solomons to determine whether temperature change

can affect gonad development in *Glycera*. The first of these took place in August, when ten worms were kept at a temperature below the average 26° C. of the water pumped into the laboratory. The arrangement for maintaining a flow of fresh water at a constant low temperature proved unstable, allowing irregular variations within a range of 12° to 20° C. After about three weeks seven of the worms had died, but all three survivors had gonads approximately twice the size of those in freshly collected worms fixed at the same time. The second attempt to observe effect of temperature change was made in January, under somewhat better conditions. Six animals were kept in separate containers placed in a cold-water bath maintained at 14° C. by a thermostatically controlled heating coil. No attempt was made in this case to provide running water to the test animals; rather, the water in the containers was changed daily. A second group of worms, serving as a rough control, was kept at about 4° C. in an aquarium supplied with running water from the pump system. After two weeks both groups were fixed. Of the six worms exposed to the higher temperature, four were in advanced stages of maturity. In these, the coelom contained well developed eggs or sperm plates, there was little or no remaining gonad tissue, and atrophy of the gut and body wall was pronounced, in two cases exceeding by far the degree of atrophy found in any of the swarming specimens examined. None of the animals kept at 4° C. showed free gametes or gonads markedly larger than those found in freshly collected worms. Although inconclusive, these results strongly suggest the importance of temperature in regulating the rate of sexual maturation in *Glycera*.

Temperature is generally regarded as a critical factor in determining the reproductive period of many marine invertebrates. Indeed, Orton (1920) concludes that other environmental conditions are of little significance. There is, however, a growing body of experimental evidence indicating that while temperature changes may accelerate gametogenesis and induce spawning, these responses depend to some degree on the physiological condition of the organism (*e.g.* Galtsoff, 1940; Loosanoff and Davis, 1952; Turner and Hanks, 1960). Furthermore, Thorson (1946) has pointed out that seasonal phytoplankton maxima cannot be excluded from the possible factors regulating reproductive activity in benthic invertebrates. Large plankton blooms in April and May, and smaller ones in September and October, have been reported for the waters around Solomons (Nash, 1947). These seasonal fluctuations occur shortly before the suggested breeding periods and hence, by augmenting the food supply, may well exert an indirect influence on the timing of reproduction in *Glycera*.

Breeding season in Canada and Maine

Klawe and Dickie conclude that bloodworms in Nova Scotia and Maine spawn only once a year, in the spring. But although they state that no observations were made in winter, it is not clear how long their observations were continued in autumn. It cannot be assumed that because two allopatric populations belong to the same species, their reproductive periods will coincide. The spawning of some nereids, for example, occurs earlier in southern than in northern latitudes, and even in the same locality, intertidal populations and those below mean sea level may spawn at different seasons (Herpin, 1926, 1928; Fage and Legendre, 1927). In addition to affecting the time of reproduction, the habitat apparently can in some

polychaetes also influence the method of reproduction (Thorson, 1950). Thus it is entirely possible that bloodworms in Canada and Maine spawn but once, whereas those further south spawn twice a year.

Nonetheless there is reason to suspect that spawning may be a biannual phenomenon for the more northern members of *G. dibranchiata* as well. Two points reported by Klawe and Dickie tend to support this suggestion. First is their observation of free oocytes in the coelom of worms examined in late August, which approximates the present findings. Their report implies that these gametes continue development through the winter and are not shed until the following spring. Although there is evidence that some invertebrates can often store ripe gametes for long periods before releasing them (Herpin, 1928; Thorson, 1946), it seems equally possible that in Nova Scotia, as at Solomons, these germ cells complete growth within a month or so and are spawned in autumn. Secondly, Klawe and Dickie mention that swarming worms, caught in a herring fisherman's net off Nova Scotia in October, 1955, were identified as bloodworms by local worm diggers, who communicated this information to the authors. But Klawe and Dickie were unable to verify this report, and since collections made in the same locality the following September yielded only swarming nereids, conclude that the diggers' identification must have been erroneous. In view of the observations from Solomons, this conclusion should perhaps be reconsidered. It may finally be mentioned that specimens originating in Maine and obtained from bait stores at Washington, D. C., in late September and early October have often contained eggs resembling in size and appearance those spawned by ripe females at Solomons.

Although final resolution of this question will depend upon confirmatory observations of spring spawning at Solomons and fall spawning in the Maritime Provinces, the present evidence permits the suggestion that *G. dibranchiata* along the Atlantic coast reproduces twice a year. Should this be correct, it will be necessary to revise the conclusions on growth rate and life span arrived at by Klawe and Dickie. These authors find that their size-frequency curves show four distinct modes, which they interpret as successive age groups. Thus the mode centering around 5 cm. represents yearling worms, that around 16 cm. represents two-year-olds, and so on, to a maximum of about 31 cm. for four-year-olds. The sudden decline in frequency of worms three years old, in comparison with the frequency of two-year-olds, is taken as an indication that most bloodworms spawn and die as they reach their third year. But as Klawe and Dickie point out, these conclusions are based on the assumption that spawning occurs only once each year. If it is in fact a biannual affair, then the modes of the size-frequency curves would represent two year-classes rather than the four proposed by Klawe and Dickie, and their consequent deductions would have to be modified accordingly.

SWARMING

Several species of *Glycera* are reported to take up a brief pelagic existence at the time of spawning (see Table I). Although Klawe and Dickie found no evidence for such behavior in *G. dibranchiata,* they suggest that bloodworms may have a short nocturnal swarming period, as do many other errant polychaetes. In an effort to check this possibility, night observations using a 150-watt bulb suspended 18–20 inches above the water were conducted from the end of the Laboratory pier at

Solomons, about 700 feet from shore, over water 8–9 feet deep. This location was chosen primarily for its convenience, but also because dredging had indicated a good concentration of bloodworms in the vicinity. More than 40 such observations were made between June and November. Most of the first 20 fell within the last half of the lunar cycle in July, August and September; the others, in October and November, included all four lunar periods. A single night's session lasted two to three hours, usually between sunset and midnight, although several observations in October and early November were conducted at times between midnight and dawn. No bloodworms appeared at the surface during any of these periods, and the observations were discontinued after the first week of November.

Dates and areas of observed swarms

Swarming of *Glycera dibranchiata* was first noticed during the afternoon of 5 November 1960 by Mr. Hayes T. Pfitzenmeyer, a member of the Laboratory staff, who brought it to the author's attention. It was witnessed again on the two following afternoons, and although no personal observations were made on November 8, reports of other staff members indicated that swarming occurred on that day also.

On November 5, swarming took place over the Middleground (Fig. 1), a shoal area approximately 500 yards east of the pier, in water 1–3 feet deep. The extent of the swarm could best be gauged by the activity of gulls, large numbers of which congregated over this area and the north shore, diving toward the water and rising with worms dangling from their beaks. This swarm lasted from about 3:00 to 5:30 P.M. and was investigated from a small boat. One of the Laboratory staff members later mentioned seeing worms on the surface at approximately 4:30 this same day while trolling in 6–10 feet of water in the vicinity of Hellen Creek; he also remarked that the stomachs of striped bass caught by him were filled with worms. Swarming on November 6 began at 4:10 P.M., in shallow water around the pier, and was again investigated by boat. Concentrations of gulls were also noticed along the north shore and to a lesser extent over the Middleground. On November 7 swarming was indicated by gulls working in the same areas as the preceding day; the boat was not used this day, and observations were limited to activity around the pier.

At the time of swarming on these four days, water temperature ranged from 12.2 to 13.8° C., and the average salinity was 14.5–14.8‰. Weather conditions were generally agreeable, except for the first day, which was overcast and rainy.

Composition and density of swarms

Ten specimens, 14 to 20 cm. long (fixed), were collected during the swarms of November 5 and 6. Only one of these was a female, but the actual sex ratio is probably less disparate. In large samples of mature worms, Klawe and Dickie found a size range of 13 to 36 cm., with males outnumbering females by only 1.3 to 1. Gravier and Dantan (1928) report lengths of 5 to 18 mm. for swarming *Glycera tesselata* and state that males were very predominant.

Although swarming activity at Solomons extended over considerable areas, individual worms were remarkably dispersed, occurring approximately 3–5 yards apart, and technically it may be questioned that the term "swarming" applies in such a case. Whether or not this dispersion is typical of spawning bloodworms,

however, remains to be seen. Apparently, pelagic breeders of other *Glycera* species have seldom been encountered in great numbers. Gravier and Dantan (1928) report collecting 25 and 48 specimens of *G. tesselata* on two different occasions, but this departs from the usual catch of one or two individuals recorded by other authors and by Gravier and Dantan for other species. The studies of Gravier and Dantan at Algiers resemble those of Fage and Legendre (1927) at Concarneau, and since in both cases observations were made shortly after sunset, these authors suggest that swarming maxima probably occurred later at night. Yet if swarming individuals of other species were as scattered as *G. dibranchiata* at Solomons, then it seems entirely possible that observations from a fixed point, such as the anchored boats used in the Algiers and Concarneau studies, would yield very few specimens, even during the height of swarming activity.

An increased density could be expected if swarming glycerids were positively phototropic and concentrated around the lamps used in nocturnal investigations. But there is little evidence indicating that *Glycera* shows a positive response to light. Although primitive epidermal photoreceptor cells have been described for some species (Stolte, 1932), members of this genus do not possess eyes, nor is there any sign that such organs develop at maturity. During some observations made at Woods Hole late in the summer of 1959, several males of *G. americana* were collected from the surface at night. These animals did not seem attracted to the light, but had apparently been carried in by the current. Experimental data are needed, however, to establish the nature of photosensitive responses in both mature and immature specimens of this group.

Swimming and shedding behavior

Swarming worms moved slowly, either at or just below the surface. Their method of swimming was completely different from that of immature animals, which advance through the water by executing a series of intricate vertical figures-of-eight, with the tail always leading the way. In contrast, swarming individuals swam head first, propelled by lateral undulations of the body. These movements resemble the type of swimming shown by *Nereis* and *Nephtys,* and it is likely that as in these genera, locomotory waves originate at the posterior end and pass forward along the body (Gray, 1939; Clark and Clark, 1960). In all observed instances the proboscis was retracted. There was no indication of any particular swimming pattern, such as the circling dances of some nereids.

Many of the worms seen at close range were shedding gametes in a steady white flow from the posterior end. Of the ten swarmers collected, two lack tail segments, and a third shows a tear in the body wall near the tail. In the intact individuals, there is a very small rupture on the dorsal surface just anterior to the pygidium. Evidently this is the avenue for gametal discharge in the majority of cases. At no time, either during swarming or in the laboratory, were gametes observed to issue from a rupture in the proboscis or anterior two-thirds of the body. However, Klawe and Dickie found that shedding in the laboratory, whether spontaneous or induced by a weak electric current, occurred with about equal frequency through the tail, the body wall or the proboscis. Judging from observation of animals spawning in the laboratory, it seems probable that a single individual releases all its gametes at one time. In a few cases, swimming activity of animals shedding in

fingerbowls was interrupted by one or two short periods of quiescence during which gametal discharge ceased. Apparently, the elimination of gametes does not require the presence of a worm of opposite sex and may well be a mechanical process resulting from the muscular pressures exerted on the coelomic fluid during swimming. This in turn would bring about a decrease in turgidity, with correspondingly weaker swimming movements until the spent animal finally sinks.

The only previous account of shedding in *Glycera* observed under natural conditions in Allen's (1957) report that pelagic breeders of *G. ?sphyrabrancha* released their gametes in two streams, apparently from pores in the midbody region. Genital ducts are not known for this genus, and gametal discharge in other species is generally presumed to occur through an oral opening left by the dissolution of the proboscis. There is no record, however, that this has ever been witnessed during actual swarming. The assumption is based primarily on the occurrence of epitokes in which the proboscis is either extremely degenerated or totally absent. With few exceptions, this condition has been found in *G. capitata, G. lapidum, G. alba, G. rouxii* and *G. tesselata* (Arwidsson, 1898; Fage and Legendre, 1927; Gravier and Dantan, 1928; Støp-Bowitz, 1941). Fragments of mature glycerids have also been collected at the surface (Fage and Legendre, 1927; Gravier and Dantan, 1928; Allen, 1957). The indications are, therefore, that shedding in *Glycera* is by dehiscence. The area of rupture probably depends on the degree of muscular atrophy, which might vary in different species.

Environmental factors

At present it is impossible to indicate the environmental agents that induce swarming in mature bloodworms or to predict the circumstances under which such behavior could be expected. Information on temperature, salinity, weather and tidal conditions was compiled from records maintained at the Chesapeake Biological Laboratory. A comparison of these data for the reported December, 1944, swarms and those observed in November, 1960, revealed no remarkable similarities. The four swarming days in both years fell between full moon and last quarter, but the significance of this cannot be established on the basis of only two reports. Swarming in 1960 began somewhat later each day, nearly coinciding with maximum high water of the second tide, and thus suggesting that tidal influences may be at least partially responsible for the daily timing of reproductive activity. Although exact hours are not available, it is known that swarming on December 4–7, 1944, took place at night (Beaven; personal communication), and hence could have been similarly associated with the second daily tide, which on those dates reached high water after dark.

A relationship between tidal conditions and onset of spawning has been reported for some other polychaetes, and in a few instances may perhaps be involved in daytime swarming (Herpin, 1926, 1928; Korringa, 1947). The regulation of gametal discharge to coincide with rising water is not difficult to understand in the case of intertidal populations. But there seems to be no ready explanation for such timing in animals not exposed at low water, especially when the tidal amplitude is small, as at Solomons. It is unlikely, however, that tidal movements alone could be responsible for stimulating swarming in *Glycera;* such behavior is more probably dependent upon the interaction of a number of factors, both environmental and physiological.

Epitoky

Almost all polychaetes that become pelagic at sexual maturity undergo some degree of structural alteration into a specialized reproductive form (see Clark, 1961). This change is known as epitoky (Ehlers, 1864–68), and the transformed individual, an epitoke. Among the Nereidae this metamorphosis often achieves remarkable complexity, resulting in the formation of a heteronereis; but in most swarming polychaetes the changes are less pronounced and generally comprise histolysis of the body musculature and the digestive tube, as well as development of additional or modified setae. Such epitokous alterations have been described for several *Glycera* species (see Table I) and appear in mature specimens of *G. dibranchiata* as well.

External appearance of epitokes

In specimens completely or partially spent, the posterior two-thirds of the body is more collapsed and darker than the anterior portion. This appearance undoubtedly results from the retention of the proboscis, which provides more bulk
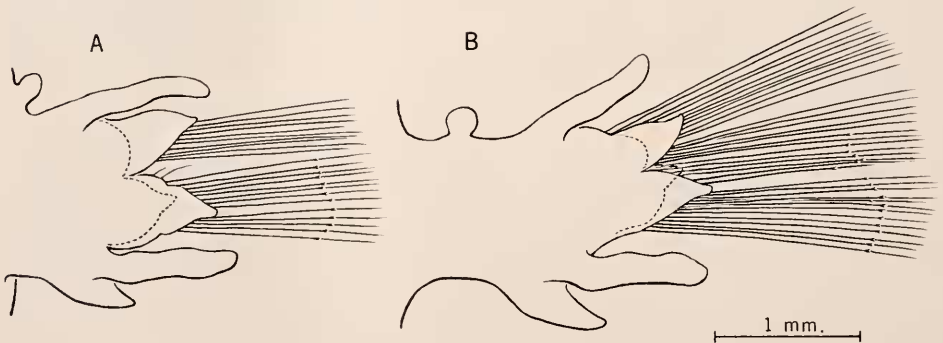

FIGURE 2. Parapod of (A) an immature specimen and (B) a swarming male. Both parapods are from the mid-body region and are shown in anterior view.

anteriorly and lacks the dark pigmentation of the gut. Parapodia of epitokes are elongated and equipped with numerous setae. In the immature parapod shown in Figure 2A, the notopodial bundle consists of 7 or 8 simple setae, and the neuropodial bundle of about 22 composite setae. Two very short simple bristles are present just dorsal to the first neuropodial seta, but since this parapod comes from a worm with large gonads, these two unarticulated setae probably represent an initial stage in the development of the mature setal complement. In contrast, the notopodial bundle of the mature parapod (Fig. 2B) consists of 19 or 20 simple setae, and the neuropodial bundle includes, in addition to 37 composite setae, 8 dorsally placed simple ones. All of these bristles are noticeably longer than those of the atokous specimen but show no structural differences.

Although the epidermis of epitokes is reduced to a very thin layer, there is a marked increase in the activity of its mucous cells, especially in the parapodial lobes. A yellow-brown pigment, also present in other tissues of mature animals,

is particularly abundant in the epidermis, where it often appears in the form of granular aggregates or minute, needle-like crystals. All the various chromogenic substances formed at epitoky probably are associated with degenerative phenomena and contribute to the coloration of mature worms. Klawe and Dickie report that male bloodworms about to spawn are a creamy color, while females are pale brown, and attribute these colors to the gametes showing through the thinned body walls. Though this may be the case in males, the eggs—being colorless—could hardly be responsible for a brown color in females. It is more likely that these differences stem rather from alterations of a metabolic nature. In the present study, color differences could be detected when mature males and females were compared in the laboratory, but it was very difficult to distinguish the sex of swarming worms in the field.

Internal changes

Epitoky is characterized by a drastic reduction in the thickness of the body wall and the diameter of the gut, with a corresponding increase in coelomic volume. Both muscle layers seem to be equally affected, but as the circular muscles are relatively thinner to begin with, this layer virtually disappears at epitoky. Since serpentine movements are executed primarily by longitudinal contractions, the difference in thickness of the muscle layers may play a role in the altered swimming behavior previously mentioned. The suspensory muscles of the digestive tube and the acicular muscles are also attenuated, though to a less striking extent. There is little apparent structural difference between muscle fibers of epitokous and atokous individuals; some vacuolization can be detected in the former, but this has occasionally been observed in immature worms as well. There is no marked invasion of the musculature by phagocytes, and in general, the epitokous condition seems to result more from atrophy than true sarcolysis.

The gut of mature animals is much reduced in diameter, with its shrunken mucosal layer appearing spongy and containing a granular yellow pigmentation. The columnar cells of this layer are apically disintegrated and have pycnotic nuclei. A scattered amorphous material occurring in the lumen probably consists of cellular debris. Despite these degenerative changes, the digestive tube, including proboscis and jaws, is entire.

The beginning of epitokous modifications in musculature and intestine appear in an ovigerous female collected 16 days before the first swarm. Since these changes are not yet visible in specimens that have just started to release gametes into the coelom, atrophy of the adult tissues may be related to metabolic requirements of the reproductive cells. Parapodial modification begins considerably earlier, before gametes appear in the body cavity. According to Støp-Bowtiz (1941), a similar sequence is found in *G. lapidum, G. alba* and probably *G. rouxii,* whereas in *G. capitata* it seems to be reversed, with degenerative changes preceding parapodial modification.

The coelomic epithelium and the septa are not affected by epitoky; nor do the segmental organs show any great change, although their protonephridial portions may be somewhat hypertrophied. The irregular black masses so numerous in the body fluid of mature worms are generally regarded as products of tissue breakdown, but their origin remains unknown. They are made up of clumped coelomic cells

containing a greenish-brown granular substance that resembles the finer granulation found in red blood cells at earlier stages of maturity. Since these corpuscles are known to contain hemoglobin (Salomon, 1941), it seems possible that the greenish-brown pigmentation may be at least partially derived from decomposition of this molecule. Raphaël (1933) proposes that hemoglobin destruction and elimination takes place in the languettes attached near the jaws and projecting into the proboscidial coelom, but does not suggest how the compound is transported to these structures. Since the reduced languettes of epitokes are not particularly pigmented, it seems unlikely that they play a significant part in hemoglobin destruction during sexual metamorphosis.

The achievement of maturity in bloodworms is further accompanied by changes in the saccular apparatus of the brain. It has previously been suggested (Simp-
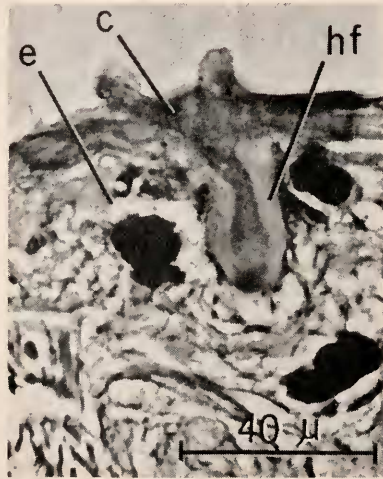

FIGURE 3. Section through the epidermis (e) on the dorsal prostomial surface of a swarming epitoke, showing the juncture of the cuticle (c) and the hyaline fiber (hf) from the saccular apparatus in the brain. The darker material within the hyaline fiber passes through the cuticle to the exterior.

son, 1959) that this structure performs a secretory function, and present observations tend to support this hypothesis. In several swarming specimens the hyaline fiber, at its junction with the cuticle on the dorsal surface of the prostomium, forms a distinct opening through which an amorphous material passes to the exterior (Fig. 3). Although this is not clearly shown in all the swarming worms examined, no sign of such an opening has been found in either the animals studied in the earlier investigation or the non-swarming specimens of the present study. It seems probable, therefore, that some type of material elaborated by or stored within the saccular apparatus is released to the exterior at the time of swarming. Histochemical tests have not been performed, but the staining reaction of this material resembles that of mucus in epidermal goblet cells, and it may well be a mucopolysaccharide similar to that previously demonstrated for the saccular apparatus. The possible significance of such an external secretion is indicated by Clark's (1961) suggestion

that neurosecretory hormones released into the water might act as coordinating factors in the spawning of some nereids.

Other modifications of the saccular apparatus also suggest an enhanced activity of this structure in worms approaching maturity as well as those fully matured. Such alterations include an increase (rarely, a decrease) in size or number of sacs, a dilation and greater convolution of the filaments, and an enlargement of the vesicles. But since these changes do not occur consistently, and since the original description of the saccular complex is based on specimens from New England, the possibility exists that such changes may represent modifications indigenous to the Solomons population and not necessarily related to reproductive functions.

Epitoky and swarming

There is considerable variation in the degree to which mature specimens are affected by epitoky, and even among worms swarming at the same time, some individuals show far less atrophy than others. Furthermore, several animals in which maturity had been induced by an elevated temperature failed to spawn even though the gametes seemed to be ripe and epitokous manifestations were more pronounced than in any of the swarming specimens. It appears that of itself epitoky does not determine the time of swarming, but that such behavior can be elicited from animals that have undergone varying degrees of metamorphosis.

The epitokous characteristics observed here are of the same type as those described for other *Glycera* species. Although in the majority of other species degeneration, especially of the proboscis and gut, is reportedly far more severe, the degree of atrophy appears to be variable in these cases also. For example, Gravier and Dantan (1928) note an exceptional swarmer of *G. tesselata* in which the proboscis is intact, and Arwidsson (1898) describes a similar instance for *G. alba*. It is possible that the November swarming observed at Solomons occurred somewhat earlier than usual, before metamorphosis had reached its peak, or, more likely, that other species as a rule achieve more pronounced epitoky before swarming than does *G. dibranchiata*.

In view of these changes at maturity, it is generally assumed that glycerids do not survive swarming. For *G. dibranchiata,* Klawe and Dickie report that the occurrence of "ghost" worms, *i.e.* the remains of dead worms, was inversely proportional to the abundance of mature individuals. No "ghosts" were found during the present study, but since swarming took place in areas not exposed at low tide, the presence of such remains would be difficult to detect. Although spent worms placed in running salt water showed movement when handled some four or five days later, they underwent gradual deterioration and in about a week's time resembled "ghost" worms. However, since the degree of atrophy at swarming appears to be variable, it is conceivable that some individuals may be able to recover after shedding.

Summary

1. This report is based on field observations made at Solomons, Maryland, between June, 1960, and February, 1961, and on histological examination of material collected during this period. It appears that bloodworms breed twice a year at Solomons: certainly during fall and very likely in late spring or early summer as well. Gametogenesis probably requires close to a year for completion. Both temperature and seasonal plankton variation are suggested as factors that may influence the timing of reproductive activity. There is reason to suspect that bloodworms also spawn biannually in the Maritime Provinces and Maine, but conclusive evidence is not available.

2. Swarming occurred mostly over shallow water, during late afternoon on November 5–8, 1960. It covered a moderately large area, but individual worms were widely dispersed. Data suggest that the onset of swarming may be coordinated with tidal conditions. Shedding is by dehiscence, through the posterior end, and is apparently an automatic process initiated by serpentine swimming movements that differ from the usual locomotion of immature animals.

3. Epitokes are characterized by atrophy of the musculature and alimentary canal, elongation of the parapods and increase in the number of setae. There are indications that the saccular apparatus of the brain releases a substance to the exterior during swarming. Although there is variation in the degree of atrophy attained at spawning, bloodworms apparently undergo less severe degenerative changes than other *Glycera* species.

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